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Fynbos plant communities and vegetation–environment relationships in the Soetanysberg hills, Western Cape

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The Cape Floristic Region of South Africa is an area of diverse substrata, high species diversity and complex vegetation patterns. Fynbos vegetation and soils were sampled at 75 sites in a 30-ha study area in the Soetanysberg hills in the south-western part of the Western Cape Province. TWINSPAN, DCA and CCA were used to investigate vegetation patterns and vegetation–environment relationships (with emphasis on soil factors). Classification of the vegetation data, which included 251 species, identified five communities associated with distinct soil types and DCA suggested two main compositional gradients. CCA showed that these two gradients were associated with environmental gradients of pH, soil depth and soil texture. When sites associated with the three substrata, namely, limestone, sandstone and colluvial sand, were analysed separately by CCA, only sandstone and colluvial sand produced significant vegetation–environment relationships. Despite the edaphic complexity of this landscape and the very large number of species, this study showed that there is predictable structure in the vegetation, related to various environmental factors, particularly at the community level.

Die Kaapse Floristiese gebied bestaan uit diverse substrata, 'n hoë spesiediversiteit en komplekse plantegroeipatrone. Fynbos plant- en grondmonsters is op 75 persele in 'n 30-hektaar gebied in die Soetanysbergheuwels van die Suidwestelike Kaapprovinsie geneem. TWINSPAN, DCA en CCA is gebruik om plantegroeipatrone en plantegroei–omgewingsinteraksies na te gaan met klem op grondfaktore. Die 251 spesies is in vyf gemeenskappe gegroepeer wat met definitiewe grondfaktore geassosieer is. Twee hoofsamestellingsgradiënte is geïdentifiseer. Volgens CCA is hierdie twee gradiënte geassosieer met grond pH, gronddiepte en grondtekstuur. Toe persele wat op die drie substrata (kalksteen, sandsteen en kolluviale sand) voorkom, afsonderlik met CCA ontleed is, het slegs sandsteen en kolluviale sand betekenisvolle plantegroei–omgewingsverwantskappe getoon. Ten spyte van die edafiese kompleksi-teit van hierdie gebied en die groot aantal spesies, dui hierdie studie aan dat, veral op die gemeenskapvlak, die plantegroeistruktuur op grond van verskillende omgewingsfaktore tog voorspelbaar is.

Keywords: Canonical correspondence analysis, colluvial sand, detrended correspondence analysis, fynbos, limestone, sandstone, TWINSPAN.

Nomenclature: Arnold & de Wet (1993).

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Introduction

The Cape Floristic Region (CFR) of South Africa ranks among the most species-rich areas of the world (Goldblatt 1978; Cowling *et al.* 1992). Regional species richness and levels of endemism of this area are comparable to those of neotropical and Asian tropical rainforests (Gentry 1986). This diversity is not reflected at the alpha level, which is only moderate (*ca.* 65 spp. in 0.1 ha, Cowling 1983; Cowling *et al.* 1992), but is most marked in the extremely high turnover between habitats, i.e. beta diversity (Cowling 1990). The prevalence of edaphic endemism in the CFR (Cowling *et al.* 1992) suggests that much of this turnover could be related to soil factors, as has been suggested for Asian and neotropical rainforests (Ashton 1969; Gentry 1988, respectively). Therefore the species richness of this region can probably be attributed to a combination of high species turnover and the geological, topographic, climatic and resulting edaphic complexity (Deacon *et al.* 1992).

Studies investigating the floristic organization of fynbos (the main vegetation type of the CFR) range from broad descriptions of major vegetation types (e.g. Taylor 1978; Campbell 1985), to detailed descriptions of communities (e.g. Boucher 1978; McDonald 1988). Soil factors appear to be of major importance in determining vegetation patterns at all levels (reviewed in Cowling & Holmes 1992). Many of the studies in which vegetation–soil relationships have been investigated, have been at the broadest level of organization or on a large geographical scale. These include studies of transitions between major vegetation types or of transects tens to hundreds of kilometres long (Cowling & Holmes 1992).

Boucher (1978) and Taylor (1984) carried out phytosociological studies in fynbos on a smaller scale (24 000 ha and 7 750 ha, respectively). They suggested that vegetation patterns were reflected in local-scale patterns of environmental factors such as soil type, moisture and slope. Various other studies have provided evidence that boundaries between fynbos communities are related to soil factors (van Wilgen & Kruger 1985; McDonald 1988). These phytosociological studies have provided qualitative descriptions of the apparent trends of community changes with environmental factors. However there is a lack of detailed, quantitative analysis of vegetation–environment relationships in fynbos.

The objective of this study was to provide a quantitative

assessment of the importance of environmental factors (related to physical and chemical soil characteristics) in explaining fynbos community patterns. The combined use of multivariate techniques, two-way indicator species analysis (TWINSPAN, Hill 1979) and detrended correspondence analysis (DCA, Hill & Gauch 1980), for such a purpose, sometimes followed by Canonical correspondence analysis (CCA, Ter Braak 1991), has become widespread in vegetation studies (e.g. Allen *et al.* 1991; Franklin & Merlin 1992; Russel-Smith *et al.* 1993).

We sampled vegetation and soil in a small (30-ha) area in a landscape characterized by much edaphic and floristic complexity. Samples were classified into communities using TWINSPAN and the compositional gradients were identified by means of DCA. CCA was then used to relate compositional gradients to a range of environmental factors.

Study area

The 30-ha study area was located about 15 km west of Cape Agulhas (34°45'S; 19°50'E) on the southern slopes of the Soetanysberg hills (249 m). The climate is fairly typical of the south-western part of the Western Cape, South Africa, namely, mediterranean-type with cool wet winters and warm dry summers. Mean annual rainfall at Cape Agulhas is 452 mm. Mean temperature of the warmest month (February) is 20.6°C and the coolest month (July) is 13.5°C.

The geology of the area is shown in Figure 1a, using the landforms described for the Agulhas Plain by Thwaites & Cowling (1988). The eastern part of the Soetanysberg hills consists of Table Mountain Group sandstone and quartzite of the Bredasdorpberge Land System, capped in places by tertiary limestone of the Hagelkraal Land System (Bredasdorp Formation), whereas the western part consists entirely of limestone (Bredasdorp Formation). Deep colluvial sand at the foot of the limestone slope is limestone derived and classified as part of the Hagelkraal Land System. The gradually deepening colluvial sand at the foot of the sandstone part of the hills, as well as the sand of the plain in front of the hills, was classified as part of the Bredasdorpberge Land System.

The vegetation types of the Agulhas Plain were classified by Cowling *et al.* (1988) using the structural-dominant species system of Campbell (1985). This system was used to provide an initial classification of fynbos types at this site (Figure 1b). On both limestone and the adjacent colluvial sand the vegetation was classified as one type of Proteoid Fynbos, including the *Protea obtusifolia–Leucadendron meridianum* community (limestone) and the *Protea susannae–Leucadendron coniferum* community (colluvial sand). The vegetation on the sandstone slope was classified as Mesic Ericoid Fynbos, with *Protea compacta*-Proteoid Fynbos on the shallower colluvial sand at the base of the sandstone slope. The vegetation on the plain classified as Dry Restioid Fynbos.

Methods

Data collection

Sampling of the vegetation took place in June and July 1992 (approximately 15 years since the last fire) along eight evenly spaced parallel transects (see Figure 1b). Ten sites, 50 m apart, were located along each transect, giving a total of 80 sites. Five sites were located in patches of vegetation which were not burnt during the previous fire in the area and therefore were at least 10 years older than the rest of the vegetation. These were excluded, leaving 75 sites.

At each site, vegetation was sampled in a 5 m × 5 m plot by visually assessing the percentage cover of all species. This plot size was selected for its efficiency when sampling many sites in a relatively small area with dense and highly variable vegetation.

Environmental data were collected at each site to cover topographical influences on micrclimate (altitude, slope, aspect), soil characteristics relevant to moisture-holding capacity (rock cover, depth and texture) and soil chemical charactersitics relating to nutrient availability (pH and a soil fertility index, integrating all soil nutrient levels and availability). Soil depth was measured by knocking a steel rod into the ground at three randomly chosen locations at each site. A single soil sample was collected at each site, from 0–10 cm depth and pH was measured in 0.01 M $CaCl_2$. After organic matter was removed by washing with H_2O_2, the coarse, medium and fine sand components of the soil were determined by sequential sieving. The soil fertility index was determined using a bioassay of radish (*Raphanus sativus* L.), a species well suited for this purpose (Olsvig-Whitakker & Morris 1982). Seeds of approximately uniform size (about 8 mg) were selected and sown in moist soil in 9-cm-diameter polystyrene pots. Because of the large number of sampling sites, only one pot with two plants was used per site (soil sample). Four seeds were sown in each pot and thinned to two seedlings where necessary. Entire plants were harvested and dried at 60°C for 48 h before weighing. To correct for growth based on seed-stored nutrients, a control of five pots with acid-washed sand was used (two plants per pot). Dry mass per plant was corrected using the control and this was used as a fertility index factor in the CCA.

Data analysis

Vegetation samples were classified using TWINSPAN, followed by ordination of sites in DCA to describe compositional gradients in the vegetation. These gradients were then related to a range of environmental factors, using CCA.

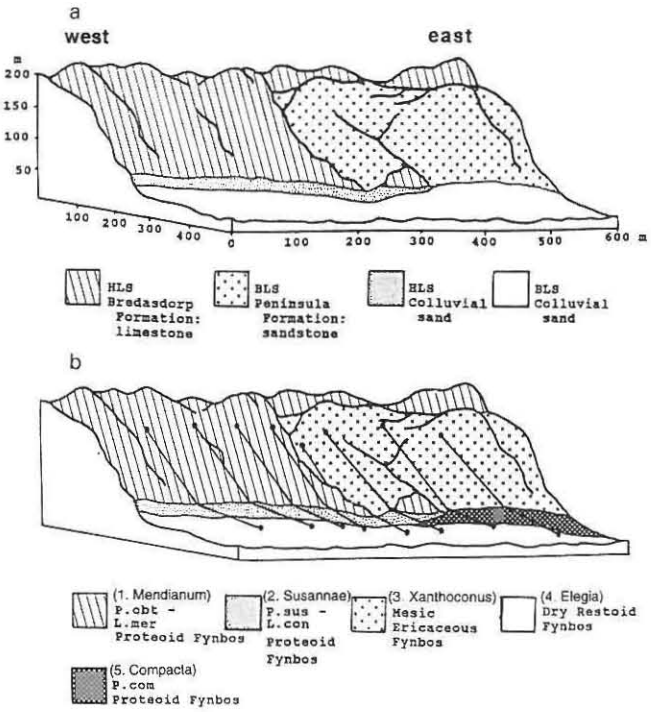

Figure 1 Diagram of the study area on the south-facing side of the Soetanysberg hills, showing (a) geology, based on the classification of the Agulhas Plain by Thwaites & Cowling (1988). Abbreviations: HLS = Hagelkraal Land System, BLS Bredasdorpberge Land System. (b) Fynbos types, based on the classification of the vegetation of the Agulhas Plain by Cowling *et al.* (1988). Abbreviations: P.obt = *Protea obtusifolia*, L.mer = *Leucadendron meridianum*, P.sus = *Protea susannae*, L.con = *Leucadendron coniferum*, P.com = *Protea compacta*. Numbers and names in brackets refer to the corresponding communities identified using TWINSPAN in this study. The locations of the eight transects along which soil and vegetation were sampled are shown in (b).

Initially, all environmental data were included in the CCA as 10 variables: altitude, slope, rock cover, soil depth, percentage coarse, medium and fine sand, pH, and fertility index, and one nominal variable, aspect, which had four classes (S-, W- and E-facing, and flat). The three soil texture factors showed high inflation factors in the CCA output, indicating multicollinearity (Ter Braak 1986). Removing the factor percentage 'fine sand' from the analysis (this did not reduce the eigenvalues of the axes) prevented the multicollinearity and thus allowed the canonical coefficients to be used for assessing the relative importance of the remaining nine factors in the analysis (Ter Braak 1986). Those variables with low regression coefficients were then selectively removed so as to produce the smallest set possible with minimal reduction of the eigenvalues. The final environmental data set which was used for the output biplot consisted of six environmental variables: rock cover, soil depth, percentage coarse and medium sand, pH and fertility index (bioassay). A Monte Carlo permutation test was used to test the significance of the eigen-values of these axes.

To compare vegetation–environment relationships on the three substrata in the study area, sampling sites were classified according to their substrata (limestone, sandstone or colluvial sand) CCA and Monte Carlo permutation tests were carried out on each data set.

Results

Vegetation classification

Classification of the vegetation data by TWINSPAN distinguished five communities (see Table 1). Each of the first three divisions of TWINSPAN separated out a distinct group of sites with at least 35% of the species restricted to that group. The remainder, with 9% unique species, was divided into two by a fourth-level division, yielding one group with 9% unique species and another with no unique species, but with different dominant species. The environmental factors corresponding to the sites where each of the five recognized communities were found are summarized in Table 2.

1. *Leucadendron meridianum–Protea obtusifolia* Proteoid Fynbos (referred to as the Meridianum community). This community included the 18 sites on limestone which were mostly on south-facing, moderately steep slopes of the limestone hills, with high rock cover and shallow soil (Table 2).The soils were fine textured with high pH and the highest fertility index. Of the 76 species in this community, 47% were unique to these sites. Dominant species were *L. meridianum* and *P. obtusifolia*.

2. *Protea susannae–Leucadendron coniferum* Proteoid Fynbos, (referred to as the Susannae community). This community included 15 sites on lightly sloping, very deep soil (see Table 2) adjacent to limestone, where it formed a distinct band at the base of the limestone slope. This soil had a high percentage of fine-textured sand, but more coarse sand than the limestone soil. It was moderately acid and of similar high fertility to the limestone soil. Of the 103 species, 35% were unique to this community, which had two distinct forms. The first occurred on the sites closest to limestone and included *Leucadendron coniferum* co-dominant with *Protea susannae*. The second occurred at sites further away from the limestone, towards the plain. The overstorey of this form also consisted of *P. susannae*, but with a low abundance of *L. coniferum*. There was an understorey of ericoid and restioid species shared with the Elegia community (community 4).

3. *Leucadendron xanthoconus–Leucospermum cordifolium* Ericaceous Fynbos (referred to as the Xanthoconus community). Although frequently dominated by proteoid species, this was classified as Ericaceous Fynbos because of the high cover of Ericaceae (Cowling *et al.* 1988). This community was found at 18 sites at higher altitude on the middle and lower sandstone slopes. These sites were predominantly on steep south-facing slopes, where rock cover was very high and soils were shallow, coarse textured, moderately acidic and had a moderately high fertility index (Table 2). This community included 124 species and dominant species, which varied substantially, included low proteoid (Proteaceae) shrubs, *Leucadendron xanthoconus, Leucospermum cordifolium* and *Aulax umbellata* as well as the broad-leaved sedge, *Tetraria thermalis*. Low ericoid shrubs constituted very high cover at all sites. Of species in this community, 39% were not found elsewhere.

4. *Elegia verreauxii–Leucospermum pedunculatum* Restioid Fynbos (referred to as the Elegia community). This community covered the 14 sites on the plain in front of the mountain and all were on flat to gently sloping terrain. These soils were very deep, with a low proportion of coarse sand, and pH and fertility were lowest here (Table 2). This community was relatively uniform across the plain and was dominated by low restioid and ericoid shrubs, especially the restoid *Elegia verreauxii* and ericoids *Staavia radiata* and *Erica imbricata*. *Leucospermum pedunculatum*, a procumbent proteoid shrub had high cover in all sites. Only six of the 64 species in this community were unique to these sites.

5. *Aulax umbellata–Protea compacta* Proteoid Fynbos,

Table 1 Number of sites and species, dominant species and character species of the five communities (based on the TWINSPAN classification)

Community			Character species	
Sites	Species	Dominant species	Include:	Total no.
Meridianum				
18	76	*Leucadendron meridianum*	*Leucadendron meridianum*	36 (47%)
		Protea obtusifolia	*Leucospermum patersonii*	
			Mimetes saxitilus	
Susannae				
15	103	*Protea susannae*	*Leucadendron coniferum*	36 (35%)
		Leucadendron coniferum	*Thamnochortus erectus*	
			Willdenowia rugosa	
Xanthoconus				
18	124	*Leucadendron xanthoconus*	*Erica monadelpha*	48 (39%)
		Leucospermum cordifolium	*Chondropetalum deustum*	
		Aulax umbellata	*Tetraria thermalis*	
Elegia				
14	64	*Elegia verreauxii*	*Gnidia pinifolia*	6 (9%)
		Leucospermum pedunculatum	*Erica cerinthoides*	
		Staavia radiata		
Compacta				
10	69	*Aulax umbellata*		0
		Protea compacta		
		Leucadendron laureolum		

Table 2 Mean values of environmental variables for the sites associated with each of the five communities. Data presented as mean ± one standard error. Tukey multiple range tests were used to identify significant differences among communities [values (within each row) with different superscripts were significantly different, $P < 0.05$]

	Communities				
	Meridianum (limestone slopes)	Susannae (base of limestone)	Xanthoconus (sandstone slopes)	Elegia (plain)	Compacta (lower sandstone slopes)
No. of sites	18	15	18	14	10
Altitude (m)	80.0 ± 5.5^{b}	44.3 ± 3.0^{c}	106.9 ± 10.2^{a}	29.7 ± 1.2^{c}	41.5 ± 2.4^{c}
Slope (°)	20.0 ± 1.8^{a}	9.4 ± 1.1^{b}	25.7 ± 2.2^{a}	1.9 ± 0.4^{b}	6.6 ± 1.0^{b}
Rock cover (%)	41.5 ± 4.3^{a}	0.0^{b}	54.5 ± 5.0^{a}	0.0^{b}	5.6 ± 3.3^{b}
Soil depth (m)	0.14 ± 0.02^{c}	1.28 ± 0.08^{a}	0.22 ± 0.07^{c}	1.39 ± 0.04^{a}	0.65 ± 0.17^{b}
% coarse sand	2.4 ± 0.5^{c}	15.0 ± 4.2^{b}	57.9 ± 2.2^{a}	15.6 ± 4.5^{b}	43.3 ± 3.6^{a}
% medium sand	31.2 ± 2.2^{ab}	34.9 ± 2.4^{ab}	16.2 ± 0.8^{c}	40.1 ± 2.9^{a}	25.1 ± 2.8^{bc}
% fine sand	66.4 ± 2.2^{a}	46.2 ± 2.4^{b}	25.9 ± 2.5^{c}	44.2 ± 2.1^{b}	31.6 ± 2.6^{c}
pH	7.23 ± 0.09^{a}	5.14 ± 0.10^{b}	5.13 ± 0.06^{b}	4.29 ± 0.23^{c}	4.90 ± 0.07^{b}
Fertility index (mg dry wt)*	46.2 ± 4.9^{a}	43.0 ± 2.9^{ab}	35.6 ± 1.5^{ab}	31.1 ± 2.1^{b}	34.1 ± 3.0^{ab}
Aspect (number of sites)					
S-facing	17	15	13	9	10
W-facing	0	0	5	0	0
E-facing	1	0	0	0	0
Flat	0	0	0	5	0

*Bioassay (see text for description)

(referred to as the Compacta community). This community consisted of 10 sites located on the gently sloping, south-facing lower sandstone slopes. Rock cover was very low and the soil was moderately deep, but shallower than the plain soils (Table 2). There was a high proportion of coarse sand and the pH and fertility index were low. Located between the Xanthoconus community on the higher sandstone slopes and the Elegia community on the plain, this community of 69 species included elements of both adjacent communities, but no unique species. It was, however, distinguished by the overstorey dominant species *Aulax umbellata* and *Protea compacta*. *Leucadendron laureolum* was dominant at some sites.

Detrended correspondence analysis

The eigenvalues of axes 1 and 2 of the DCA for the sites were 0.86 and 0.55 respectively (Figure 2). Sites belonging to four of the communities classified by TWINSPAN (Meridianum, Xanthoconus, Elegia and Compacta) were clustered in the ordination. Sites belonging to the fifth community, Susannae, were more widely dispersed. The 75 sites were arranged into three main groups consisting of the Meridianum community, which was widely separated from the others, the Susannae community and a third group consisting of the Xanthoconus, Compacta and Elegia communities (the latter two communities were largely overlapping). The first two DCA axes suggested two main compositional gradients in this vegetation. Along axis 1, the sequence was from the Meridianum community to the Susannae community, followed by the Xanthoconus, Compacta and Elegia communities (which shared species and were not distinguished along this axis). This sequence corresponds to a pH and fertility gradient (see soil characteristics associated with each community, in

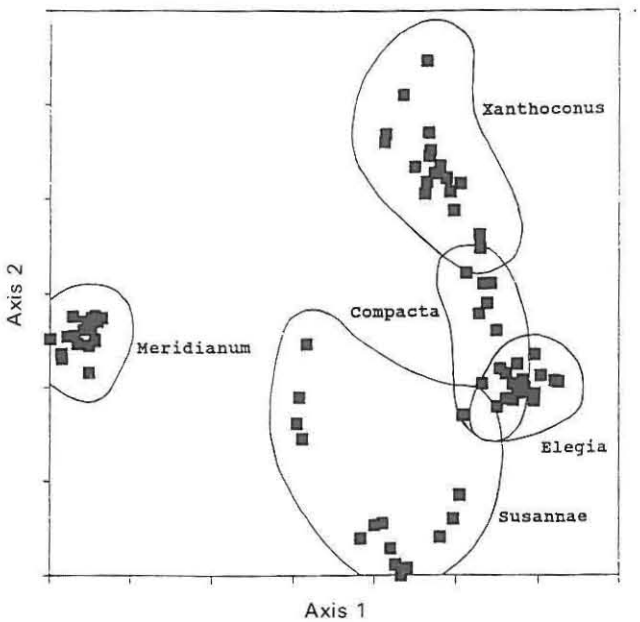

Figure 2 DCA ordination diagram for 75 sites, plotted on the first and second axes. The groups of sites associated with each of the five communities are circled and labeled.

Table 2). The Meridianum, Susannae and Elegia communities were not separated along axis 2. The main compositional gradient along axis 2 was from the Elegia and Compacta communities to the Xanthoconus community, which was fairly widely dispersed along this axis. Although this sequence was not as clear as that along axis 1, it corresponds to some extent with decreasing soil depth (see Table 2).

Canonical correspondence analysis

Complete data set

The complete data set, incorporating all environmental factors, produced eigenvalues of the first two CCA axes of 0.82 and 0.65. Table 3 shows the canonical coefficients of all environmental factors (except for fine sand which had been omitted to prevent multicollinearity). The highest coefficients, indicating the main determinants of the CCA axes, were for pH (axis 1) and soil depth (axis 2). Soil texture (% coarse and medium sand), percentage rock cover and fertility index (bioassay) had lower coefficients. Altitude and slope were only of minor importance, despite substantial differences between communities. The nominal variable aspect had very low influence, as the majority of sites were south-facing. Removal of factors with very low regression coefficients, namely, altitude, slope, aspect and fine sand, produced no reduction in the axis 1 eigenvalue and only reduced that of axis 2 by 0.01 to 0.64. Any further removal of factors produced more rapid decreases in the eigenvalues and so a set of six was selected as the best set. These were pH, soil depth, rock cover, % coarse sand, % medium sand and fertility index.

Table 3 Eigenvalues and canonical coefficients of the first and second CCA axes of the complete data set and eigenvalues and inter-set correlation coefficients for the sandstone and colluvial sand data sets. No results are shown for the limestone data set as the axes were not significant

	Complete data set		Sandstone		Colluvial sand	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalues	0.82	0.65	0.47	0.22	0.73	0.41
Environmental variables: coefficients						
Altitude	0.02	0.12	–0.74	0.42	0.79	0.47
Slope	0.10	0.10	–0.81	–0.24	0.60	0.47
Rock cover	–0.02	0.17	–0.81	–0.23	–0.10	0.32
Depth	–0.14	–0.51	0.31	0.25	–0.06	–0.68
% coarse sand	–0.36	0.11	*	*	–0.02	0.64
% medium sand	–0.13	–0.17	0.34	–0.05	*	*
% fine sand	*	*	0.11	0.46	0.11	0.49
pH	0.71	–0.30	–0.03	0.34	0.79	0.07
Fertility index	0.03	–0.15	0.55	0.32	0.72	–0.29
Aspect						
S-facing	–0.02	–0.05	–0.33	0.17	–0.12	0.11
W-facing	–0.01	–0.05	0	0	+	+
E-facing	–0.03	–0.05	+	+	+	+
Flat	0	0	+	+	0	0

* Variable was excluded from analysis to prevent multicollinearity (see text)

\+ These values of the nominal variable aspect were not represented in this data set

The biplot of 75 sites (site positions in the plot being the weighted averages of their component species) and six environmental factors is shown in Figure 3. The first two axes explained 16% of the variance in the species data. Despite this low value, a Monte Carlo permutation test of the F-ratios of the axis 1 eigenvalue and the trace statistic showed both to be significant ($P < 0.05$). The groups of sites for each of the five communities (classified by TWINSPAN) were clustered in a manner very similar to that in DCA. The arrangement of these community groups along the CCA axes was also very similar to the arrangement on the DCA axes. Axis 1 separated the Meridianum community from the others along what was predominantly a gradient of increasing pH, although soil texture (decreasing percentage coarse sand) was also important. The separation of the Meridianum community sites from all the others was more pronounced than in the DCA (resulting from major soil differences).

On axis 2, sites were dispersed along a gradient of decreasing soil depth in the sequence of Susannae and Elegia communities, followed by the Compacta community and finally the Xanthoconus community in the shallowest soil. There was also a gradient of decreasing percentage medium-textured sand and increasing coarse-textured sand.

Single substratum data sets

The limestone data set consisted of 18 sites and 76 species. The vegetation of all of these sites was classified as the Meridianum community. These sites varied substantially in altitude, slope, rock cover and fertility index (see standard errors in Table 2), but no significant vegetation–environment relationship was detected (Monte Carlo permutation test).

The sandstone data set included 23 sites and 141 species. When the CCA with all environmental factors was carried out, it

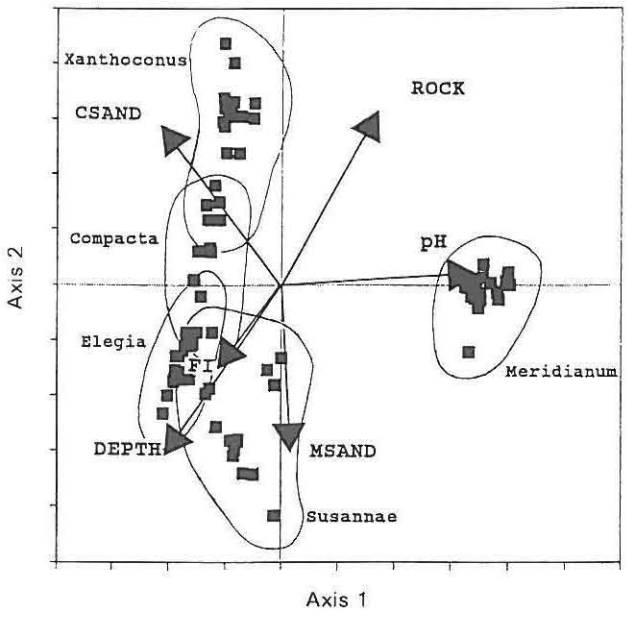

Figure 3 CCA biplot of site scores for 75 sites and the set of six most important environmental factors (vectors) on the first two CCA axes. The environmental factors were: pH, ROCK = % rock cover, CSAND = % coarse sand, FI = fertility index, DEPTH = soil depth and MSAND = % medium sand. The groups of sites associated with each of the five communities (from the TWINSPAN classification) are circled and labeled.

produced eigenvalues of 0.47 and 0.21 (for axes 1 and 2 respectively). Percentage coarse sand was omitted to avoid multicollinearity (the eigenvalues were not influenced by this). The effect of aspect was uncertain, as 18 sites were S-facing (correlation coefficient: 0.33). The remaining five were W-facing and this had a coefficient of 0.0. The overall importance of aspect in the vegetation–environment relationship was apparently minor, because when this was eliminated from the CCA, the first axis eigenvalue dropped by only 0.03 and the second axis eigenvalue remained unchanged. The first two axes of the CCA with the final set of eight environmental factors (Figure 4a) explained 22% of the variation in the species data. The trace statistic (sum of all eigenvalues) was significant ($P < 0.05$), but the first eigenvalue was not significant on its own. The canonical coefficients did not correspond with the biplot scores for the environmental factors and so inter-set correlation coefficients were used to determine the relative importance of each factor (Table 3). These are correlations of environmental variables with species axes and provide an alternative means of assessing the importance of the environmental factors when the canonical coefficients cannot be used (Ter Braak 1986). The factors best correlated with the first CCA axis were slope, rock cover, altitude and fertility index and, to a lesser extent, percentage medium sand and soil depth. For axis two, all correlations were much lower and the highest coefficients were for percentage fine sand and pH. The biplot (Figure 4a), showed the sites of the Xanthoconus community to be widely dispersed along both axes, with the five Compacta community sites separated from those of the Xanthoconus community along axis 1 (lower altitude, rock cover and shallower slope).

The colluvial sand data set comprised the largest of the single substratum data sets, with 34 sites, 138 species and three out of the five communities. This produced higher eigenvalues than the sandstone sites: 0.73 for axis 1 and 0.41 for axis 2, with percentage medium sand removed to prevent multicollinearity. Aspect was also removed, as 29 sites were south-facing and five were on level ground. This reduced the axis 1 eigenvalue by only 0.02 and did not influence the axis 2 eigenvalue. The first two axes of this analysis explained 24% of the variation in the species data. Both the axis 1 eigenvalue and the trace statistic of the CCA with eight environmental factors were significant ($P < 0.05$). As with the sandstone data set, it was necessary to assess the importance of the environmental factors on the basis of interset correlation coefficients (Table 3). High coefficients were found for altitude, pH, fertility index and slope in axis 1, and for depth and percentage coarse sand in axis 2.

In the biplot (Figure 4b), sites representing the Elegia, Compacta and Susannae communities were arranged sequentially along axis 1. This represents what was primarily a nutrient gradient (increasing pH and fertility). This gradient was also associated with increasing altitude. Most of the dispersion of sites along axis 2 occurred with sites in the Susannae–Coniferum group, as well as the Compacta community. This was the result of a gradient of depth and soil texture (percentage coarse sand) along with altitude and slope.

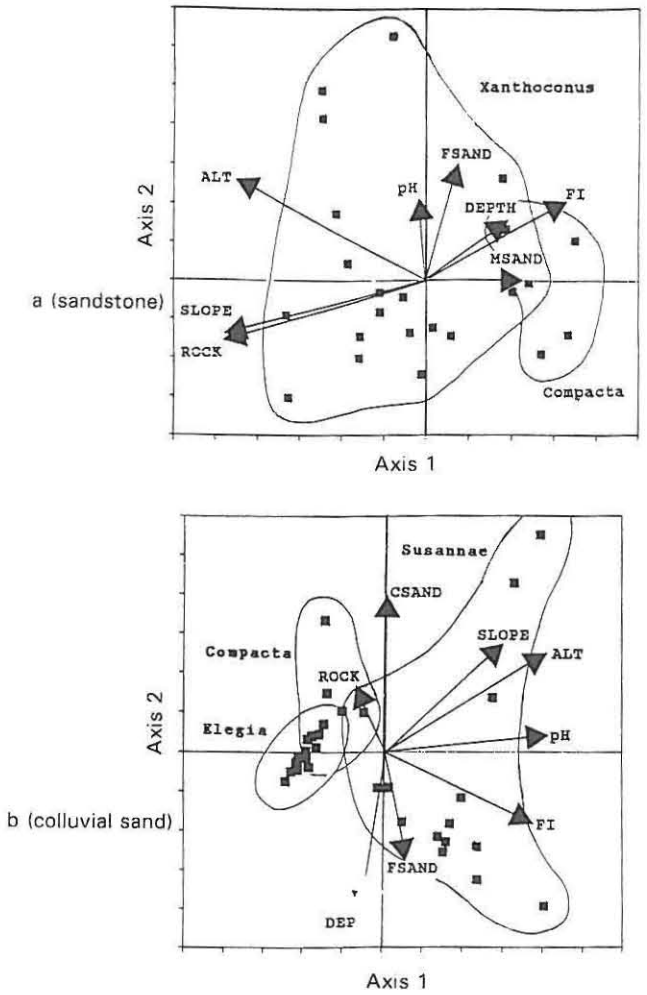

Figure 4 CCA biplots of sites on (a) the sandstone substratum (23 sites) and (b) the colluvial sand substratum (34 sites). Environmental factors were: ALT = altitude, SLOPE, ROCK = % rock cover, DEPTH = soil depth, FSAND = % fine sand, MSAND = % medium sand (sandstone only), CSAND = % coarse sand, (colluvial sand only), pH and FI = fertility index (see text for determination). Groups of sites belonging to different communities (two on sandstone and three on colluvial sand) are circled and labeled.

Discussion

The species richness of fynbos is substantially higher than most vegetation types where multivariate analyses such as DCA and CCA have been applied (for example, Haase 1990; Allen *et al.* 1991; Franklin & Merlin 1992). This study of vegetation–environment relationships in fynbos took place on a much smaller scale than all the above studies, but in spite of this, a strong vegetation–environment relationship was shown to exist. Not only were there many species in a small area, but they were found to be grouped into distinct communities with varying degrees of spatial overlap or numbers of shared species. The CCA showed that the two main compositional gradients (community changes across the landscape) were strongly correlated with gradients of soil factors, namely pH and a physical gradient consisting of soil depth and texture. Although soil fertility did not emerge as a major factor, the importance of pH is evidence of the key role of soil chemical characteristics in this area, as suggested by Cowling (1990) for the Agulhas Plain as a whole. The importance of soil depth and texture relates to the importance of soil volume and texture on moisture availability, and consequently on nutrient availability (Yair & Danin 1980; McConnaughay & Bazzaz 1991). Soil moisture is of particular importance during summer drought in mediterranean-climate regions such as this (Miller *et al.* 1983).

Limestone is a relatively rare substratum in the Cape Floristic Region (Deacon *et al.* 1992) and the associated vegetation has an extremely high level of endemism (Thwaites & Cowling 1988; Cowling *et al.* 1992). Despite the high proportion of limestone-restricted species (47%), the structure and generic composition of the limestone fynbos differed very little from the surrounding acid fynbos. In the CCA, the sites with the Meridianum commu-

nity were distinguished on the basis of pH and not fertility. This was probably because the limestone sites were extremely variable in fertility (including both the highest and lowest values). Although these soils are high in total nitrogen and phosphorus (Thwaites & Cowling 1988; Richards 1994) availability of these nutrients, especially phosphorus, would be greatly reduced through organic and inorganic immobilization (Stewart & Tiessen 1987; Witkowski & Mitchell 1987).

The failure to detect a significant vegetation–environment relationship within the limestone substratum is not surprising as it included only one community. However, this is in spite of relatively substantial variation in environmental factors (altitude, slope, rock cover, fertility). A general feature of these limestone soils is that with the very high rock cover, the soil occurs in thin sheets over rock and in pockets or fissures. Such patterns have major implications for soil moisture availability (Yair & Danin 1980) and consequently on nutrient availability (McConnaughay & Bazzaz 1991). It is possible that soil characteristics relating to depth and volume influence the distribution of species on limestone, but at a scale smaller than that detected using 5 m × 5 m plots.

In contrast to limestone, the sites on sandstone showed a significant vegetation–environment relationship. Altitude and slope, which did not emerge as important factors in the complete analysis, were found to be important on sandstone where they were most variable. The strongest factors were the physical variables related to soil moisture, i.e. soil depth, texture and rock cover. Factors relating to nutrients (pH and soil fertility) were of lesser importance and were fairly uniform across this substratum. The overriding importance of physical factors relating to soil moisture availability has been widely supported for sandstone mountain fynbos in general (Cowling & Holmes 1992). The Xanthoconus community on the higher, steeper slopes (differentiated from the Compacta community at the base of the slope) belongs to the Mesic Ericaceous Fynbos type, dependent on this microclimate of steep, seaward-facing slopes on coastal mountains with increased orographic rainfall and exposure to fog (Campbell 1985; Cowling *et al.* 1988).

The colluvial sand data set was fairly complex in terms of the range of environmental factors and vegetation (although there was much overlap between the three communities) and produced the strongest vegetation–soil relationship of all three substratum types. It also included some of the most fertile sites in the landscape (adjacent to limestone), as well as the most acid and infertile sites (on the plain). This resulted in a strong correlation of the fertility index with variation in the vegetation (an effect obscured in the complete analysis) and a slightly greater role for pH than on sandstone. Two main compositional gradients on colluvial sand were from west to east (Susannae to Compacta communities), associated with the environmental gradients of soil depth, pH and fertility, and from north to south (Proteoid Fynbos at the base of the hill, to Restioid Fynbos on the plain) along an environmental gradient of altitude, slope, pH and fertility.

The vegetation–environment relationships described above explained much of the compositional pattern in the vegetation, especially with regard to the communities. However, only 16% of the variance of the species data in the complete data set was explained, whereas 22% and 24% were explained by the first two CCA axes in the sandstone and colluvial sand data sets respectively. Ter Braak (1991) pointed out that low explained variance is typical of species-abundance data in CCA analyses, resulting from the frequently high noise levels in such data. The fact that the eigenvalues of the CCA axes were similar to those in the DCA is evidence that an appropriate set of environmental factors was used (see Franklin & Merlin 1992). Nevertheless, there are certain additional explanations that should be considered.

(i) Additional environmental factors, not considered here, include organic carbon content of soils which varied substantially in the landscape (Richards 1994), individual nutrient factors (micro- and macronutrients) and factors which vary with time. These include available nitrogen and phosphorus, levels of which vary greatly during the year, influenced by moisture, temperature, pH and Ca (Witkowski & Mitchell 1987; Stock *et al.* 1988).

(ii) In fynbos almost all recruitment occurs after fire and, for many species, this is from seed (Kruger 1983). Fire differentially influences species distribution patterns by causing local extinctions and population explosions (Cowling 1987). The immediate post-fire environment may also differ from later stages in terms of spatially varying fire-induced changes in nutrient availability (Stock & Allsopp 1992).

(iii) Biotic interactions, such as competition and predation, which could influence species distributions were not considered in this study. Predation of seeds and seedlings has been shown to influence vegetation boundaries (Brown & Heske 1990). The importance of interspecific competition in influencing community composition and community boundaries is a subject of much ecological research recently (see reviews: Keddy 1989; Bond *et al.* 1992). However, understanding the importance of a process such as competition and its interaction with environmental factors requires manipulative field experiments (Keddy 1989).

In conclusion, this study area, although small, is unusual in both its species richness and the fact that it includes a wide range of soil types representative of those on which fynbos is found. The distinct communities present in this vegetation showed compositional gradients that were strongly correlated with environmental factors. This relationship of complex patterns of vegetation and environmental factors is convincing evidence of the crucial role that environmental factors, especially soil factors, play in determining species distributions, beta diversity and ultimately, the enormous species richness of the Cape Floristic Region.

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